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THE COLOR SENSE OF THE HONEY-BEE: IS CONSPICUOUSNESS AN ADVANTAGE TO FLOWERS?

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In 1895, Professor Felix Plateau, of the University of Ghent, began the publication of a long series of papers, in which he asserted that Hermann Müller, in formulating his theory of the evolution and use of floral colors, had been misled by a too vivid imagination; and that anthophilous insects are attracted chiefly by odor. In a list of his papers prepared by himself and now before me Plateau states that his latest contribution, entitled Les insects et la couleur des fleurs,[1] contains a "summary of the whole." The conclusions of many years of patient research are given at the close of this paper as follows:

> "In the relations between the insect fertilizers and entomophilous flowers, the more or less bright coloration of the floral organs has not the preponderating rôle which Sprengel, H. Müller and their numerous adherents have attributed to them. All the flowers in nature might be as green as the leaves without their fertilization being compromised. The sense of smell so well developed among most insects far from being a secondary factor is probably the principal sense which discovers to them the flowers containing pollen and nectar."

By fertilization Plateau doubtless means pollination, for fertilization is an entirely distinct phenomenon, often not occurring until many months after the pollen has been placed upon the stigma. Plateau's conclusions have not met with general acceptance; and in some instances, as he himself naïvely remarks, have been criticized in a "merciless manner."

Florœcology is, however, greatly indebted to him not only for many very interesting observations and experiments, but also for insisting that the whole subject of the relations of insects to the colors of flowers should be reexamined and tested experimentally. With the exception of the criticisms of Bonnier, in 1879, Müller's doctrine had remained unquestioned, for no other theory of the significance of brilliant floral leaves is so satisfactory as that they serve as signals or flags to attract the attention of anthophilous visitors. It is well to recall that the great authority, which has been attached to the name of Müller, rests on innumerable observations and collections, which were continued up to the morning of his sudden death from a pulmonary complaint while studying the flowers of the Tyrol. He is still justly regarded as the foremost of florœcologists. Says his biographer Ludwig:

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[1] Plateau, F. Les insects et la couleur des fleurs. *L'Annêe Psychologique,* 13, 67–79, 1907.

> "He is not dead, he lives and will live so long as a flower enraptures the eye of an investigator. His bright spirit will live on and, we hope, like that of his teacher and friend Darwin long be a light on the way to truth in the heart of nature."[2]

Plateau's first paper dealt chiefly with the concealment of the flowers of the dahlia with green leaves; and his second, which appeared in the following year, with the removal of petals. In the last-named communication he describes how he removed the larger part of the corolla of *Digitalis purpurea, Lobelia erinus, Œnothera biennis, Ipomœa purpurea, Delphinium ajacis,* and *Antirrhinum majus;* and with the exception of *A. majus* found that the inconspicuous stumps were visited by insects almost as frequently as the unmutilated flowers.[3] He, therefore, concluded that neither the color nor the form was important, and that insects were attracted by the fragrance alone. I shall again refer to these experiments after relating my own, which gave very decisive results diametrically opposed to those of Plateau.

[2] Ludwig, F. Das Leben und Wirken Professor Dr. Hermann Müller's. *Botanisches Centralblatt,* 17, 404, 1884.

[3] Plateau, F. Comment les fleurs attirent les insects, II. *Bul. Acad. roy., Bruxelles,* 32, 504–34, 1896. I have not been able to obtain this paper, the reprints being exhausted. The experiments are described, apparently with sufficient detail, in Knuth's Handbook of Flower Pollination, and it is upon this account that I have depended.

To determine the influence of the petals of the common pear, *Pyrus communis*, upon the visits of the honey-bee, *Apis mellifera* L., a medium-sized tree in full bloom was selected for observation. The day was clear, warm and calm, the bees were numerous and no other insects were present.

A cluster of seven blossoms near the end of a branch was watched for fifteen minutes and received eight visits of the honeybee. The petals were now all removed and it was observed for a second quarter of an hour. Though a number of bees flew near by, it received not a single visit. During a third fifteen minutes there were two visits, due in part to association, for the bees came from other blossoms on the same tree, which had proved the first source of attraction.

Two other clusters of flowers, growing side by side but nearer the bole of the tree, consisting each of eight flowers, were observed for fifteen minutes and sixteen separate visits of the honeybee were noted The petals of one of these clusters were now removed. During fifteen minutes the adjacent cluster, which still retained its petals, received eleven visits, while not one was made to the cluster without petals. In one instance a bee hovered over it but did not alight.

These results were much more conclusive than I had expected; for, in the second experience, it might have been supposed that the odor exhaled by the evaporating nectar of the denuded blossoms would have attracted the bees, which were only an inch or two distant; but their movements were evidently determined almost entirely by the presence of the petals.

On a warm pleasant morning in August at 11:30 o'clock, (A.M., I selected for experiment two groups of flowers belonging to *Borago officinalis*, or the common borage. They were distant apart about six inches; one contained five flowers; the other, which was at a little higher elevation, contained four flowers. They were both watched for ten minutes. The first received fifteen visits from the honey-bee, the second thirteen visits. The location of my apiary not far away furnished a large and continuous supply of visitors. The rotate corollas, together with the cone of black anthers, the stamens being attached to the base of the petals, were now removed from the five flowers of the first group. There remained the green calyx, the pistil, and the green disc surrounding it which secretes the nectar. The two groups were now observed for a second ten minutes, the first received no visits, the second seven visits from the domestic bee as previously. Once a bee hovered around the denuded flowers of the first group but failed to alight. The much smaller number of visits made to group number two during the second interval may in part have been due to the less conspicuousness of the whole patch of flowers. There were scattered upon the ground many partially withered corollas and twice a bee was seen to fly down toward them. With a lens of twenty diameters I examined three of the defoliated blossoms and in two of them found eight or nine small drops of nectar, so that had a bee alighted upon them it would have been richly rewarded for its discernment. The flowers possessed no perceptible odor. Three points in the second part of this experiment should be carefully noted; first, that the flowers from which the corollas had been removed, though they contained an abundance of nectar, received no visits; second, that the flowers left complete received a much less number of visits than during the first interval; third, that the bees were attracted by the wilting corollas lying upon the ground.

On August 14, I made the following experiment upon a staminate flower of the garden squash, *Cucurbita maxima*. The weather was clear and warm. During an observation of ten minutes it received twelve visits, eight of which were made by honey-bees and four by workers of *Bombus terricola* Kirby. The perianth was then removed close to the cup-shaped reservoir, but the denuded flower with its prominent club of stamens and yellowish disc was still a conspicuous object though much less so than before. It was watched for a second ten minutes and received only one visit, from a bumblebee (*Bombus terricola*). During the first interval no visit was counted that the bee did not enter the corolla and go down to the honey receptacle. Within a few inches of this "stump" and a little lower down there was another squash flower, the corolla of which had wilted and was nearly closed. During the second ten minutes this flower received five visits,[4] two from *B. terricola* and three from honey-bees, though they were unable with a single exception to find an entrance. There can be little doubt that had the corolla been present on the first flower these bees would have entered it.

On the fifteenth, the weather being favorable, the experiments on the flowers of *Cucurbita maxima* were continued. Two flowers, both staminate, growing side by side, their corollas touching, were selected. Number one appeared rather older than number two, which had evidently expanded very recently. Both were observed for ten minutes. Number one received six visits, four from *Bombus terricola,* two from the honey-bee; while number two received thirteen visits, all from bumblebees (*B. terricola*). The fresher condition of this flower probably accounted for the larger number of visits. Both the calyx lobes and the corolla were now cut away from number two, the most attractive flower, leaving only the disc and the monadelphous club of stamens. This was by no means an inconspicuous object, as the yellowish disc is 15 mm. in diameter, and the yellow anthers are over 2 cm. long. The two flowers were watched for ten minutes. No visits were made to number two; but number one received twelve visits, six from honey-bees and six from *B. terricola*. It is evident that the corolla was a great advantage, and that number one suffered in competition with number two, the number of visits to number one greatly increasing when number two was rendered comparatively inconspicuous. Shortly after this experiment was completed a honey-bee was seen to visit the decorollated flower of number two; and inserting its tongue through one of the narrow slits in the top of the cup-like receptacle it remained sucking for two minutes, finding evidently an ample quantity of nectar. It then visited flower number one, but its further flight was not followed. A moment or two later a honey-bee was again seen on the nectar receptacle of number two, which was doubtless the same individual, for its subsequent flight was followed and it returned twice afterwards, finding the nectar here more abundant than in the complete flowers. Later a fifth visit was observed, probably by the same bee. There were many more bumblebees present than honey-bees, and the greater capability of the honey-bee in finding the nectar and in making the most of its discovery is noteworthy. During this whole time number one, from which the corolla had not been removed, continued to be frequently visited by bees. The corolla of the squash possesses an agreeable fragrance, but the defoliated flower also exhales a strong though coarser and more weed-like odor. The visits were recorded on the instant they were made.

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[4] The bees alighted upon the corolla and tried to enter it.

In these experiments the visitors were not a miscellaneous group of insects belonging to several orders and differing widely in their habits of visiting flowers and, according to Müller, in their color sense; but the flowers of *Pyrus communis* and *Borago officinalis* were visited by *Apis mellifera* alone, and of *Cucurbita maxima* by *Apis mellifera* and *Bombus terricola,* allied species, which are placed by some authors in the same family. The visits were purposive and not ambiguous, as is not infrequently the case with the visits of many diptera and even of the less specialized bees. To the complete flowers the number of visits were numerous and decisive. On the contrary, they ceased almost entirely to the decorollated flowers, though they contained an ample supply of nectar; while at the same time in the control observations made for the purpose of comparison they continued numerous. The few exceptions may be explained by the odor of the evaporating nectar, and by the tendency of bees to return habitually to a place where they have once obtained food. That the white, blue and yellow corollas were beneficial to the flowers of their respective species does not admit of question. To attribute this advantage to any other cause than conspicuousness would appear to be a perversion of the facts.

Let us again refer to Plateau's experiment with *Digitalis purpurea*. The larger part of the tubular corolla was cut away leaving a cup-shaped stump 1 cm. long, which was visited by two bees, *Bombus terrester* L. and *Anthidium manicatum* L., nearly as frequently as when the flower was complete. Knuth suggests that the nectar now being exposed to the sunshine and wind must evaporate more rapidly, give out a stronger odor, and should attract more insects than when it was concealed at the bottom of the long corolla-tube. As this was not the case, he holds that the uselessness of the bright corolla was not proved. I should explain the continuation of the visits of the two species of bees as follows. A cup-shaped flower 1 cm. long is by no means very inconspicuous *per se*. The bees had already visited these flowers and learned that they contained nectar; and they would come again to the same place in accordance with their well-known custom of returning habitually to a locality where they have once procured food. They would find smaller, more open flowers with perhaps a stronger odor; but that insects with the keen discernment of bees should be greatly deceived by this change is highly improbable. The results observed by Plateau in the excision of the corolla of *Digitalis purpurea* are precisely those which would have been expected. The force of this objection occurred later to Plateau himself in the case of flowers masqued with green leaves, as when he enveloped with the leaves of rhubarb the inflorescence of Heracleum, for he says:

> "Or, j'ai effectué en 1895 et 1896, aux débuts de ma longue serie de recherches sur les rapports entre les Insects et les fleurs, des expériences

que l'on n'a certainement pas oubliés et dan lesquelles je constatais de multiples visites d'Insects à des fleurs dont toutes les parties colorées étaient cachées par du feuillage. L'objection que les résultats de ces expériences ancienne étaient précisément et exclusivement dus au souvenir de l'emplacement se présente immédiatement à l'esprit."

"Je reconnais bien volontiers que cette objection frappe juste pour certaines des expériences en question."[5]

But in my experiments with the heads of simple dahlias masqued with grape-leaves, Plateau continues, the memory of a place visited habitually does not wholly explain the behavior of the insect visitors. In some instances he covered up only the disc florets, leaving the ray florets exposed; in others he covered the entire upper face of the capitulum, both ray and disc florets, but not the under side, with green leaves, and both bees and butterflies (species of Bombus, Megachile, Pieris and Vanessa) continued to fly toward the inflorescences and often found the pollen and nectar by creeping under the covering of leaves. Plateau concludes that the rays do not act as signals, and that the form and bright colors of the capitula of dahlias are not an important influence in attracting insects.

These conclusions are disputed by Forel, who in the following interesting experiment shows that bees in their visits to covered dahlia heads are guided by both memory and sight.[6] In a dahlia bed containing forty-three floral heads of different colors he covered up twenty-five with grape-leaves bent around them and fastened with pins. Of four others he covered only the discs, while of one he covered the rays, leaving the disc visible. The bees were so numerous that at times there were two or three to a flower. The bees ceased at once to visit the completely covered heads; they continued, however, to fly to the heads with only the discs covered, though they immediately abandoned them, except in a few instances where they succeeded in finding the central florets beneath the leaves; but to the dahlia with the disc exposed and the rays covered they continued to fly as usual. But the bees remembered the earlier condition of the dahlia bed and seemed to be seeking the dahlia heads which had so suddenly disappeared. Soon a poorly concealed specimen was detected and visited, then another, and at the end of about three hours the entrances at the side and below were discovered and the hidden flowers were again being visited. Forel says:

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[5] Plateau, F. Note sur l'emploi de recipients en verre. *Bul. Acad. roy., Bruxelles*, No. 12, pp. 741–75, 1906. Vid. pp. 771–2.

[6] Forel, August. Ants and Some Other Insects, translated by William Morton Wheeler. The Open Court Publishing Co., Chicago.

> "Plateau, therefore, conducted his experiments in a faulty manner and obtained erroneous results. The bees still saw the Dahlias which he at first incompletely concealed. Then, by the time he had covered them up completely, but only from above, they had already detected the fraud and saw the Dahlias also from the side. Plateau had failed to take into consideration the bees' memory and attention."

To Forel's criticisms published, in 1901, in *Rivista di Biologia Generale*, Plateau has replied in part: That not only bees but numerous diurnal lepidoptera visited the masqued dahlias, and that while it was freely admitted that insects could see the under side of the covered capitula and the radiating form and red or rose color of the floral ligules, yet they were without attractive value, as it was only very rarely that an insect approached the inflorescence of this side.[7] To these statements I will again refer later. His further explanations as well as his assertions that his opinions have in some particulars been misunderstood by Forel are immaterial to the present discussion. But in admitting that the visits of hymenoptera can be partially explained by memory Plateau practically abandons his position so far as his experiments with dahlias are concerned.

Forel, as has already been mentioned, points out that Plateau has attached too little importance to the bee's memory and attention. These are, indeed, qualities more likely to be appreciated by the practical apiarist than the entomologist. A single example will suffice to show the strength of the bee's memory for location. During September and the early part of October, while carrying on various observations, I accustomed honey-bees to visit the window of my library for honey and sugar syrup, and now nearly a month and a half later, though they have not been fed since, they still continue to return whenever warmer weather permits. I have little doubt that when the winter is past and they resume flight in April, as in the experience of Huber, they will come again. I shall certainly expect them.

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[7] Plateau, F. Note sur l'emploi de recipients en verre. *Bul. Acad. roy., Bruxelles*, No. 12, pp. 772–75.

The great perseverance and power of observation exhibited by bees, when searching for nectar in a locality where they have previously procured it, is likewise well illustrated by Forel's experiment. For more than three hours they continued to look for the missing dahlia flowers, until finally they detected a way to reach them under the leaves. This acuteness of sense is also well shown in the following experiment, which I performed on October 6 after most of the natural flowers had perished.[8]

I accustomed a number of bees to visit a red glass slide, 3 inches long by 1 inch wide, on the center of which was a small quantity of honey The slide was placed in the sunlight on the top of a white box about two feet high. A second white box was then placed fifteen feet from the first and to this the red slide was removed. A bee found the honey at the end of six minutes and a few seconds later another came. In ten minutes there were four bees. During this interval the bees were continually flying around the first white box. I now removed the second white box but left the first undisturbed. An hour later

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[8] It is instructive to compare this experiment with one described by Lubbock, where the attention of the bees was preoccupied. ''I placed a saucer of honey,'' he says, ''close to some forget-me-nots, on which bees were numerous and busy; yet from 10 A.M. till 6 only one went to the honey.'' (''Ants, Bees and Wasps,'' p. 280.) ''Attention is surprisingly developed in insects,'' says Forel, ''often taking on an obsessional character and being difficult to divert.'' (''Ants and Some Other Insects,'' translated by William Morton Wheeler, p. 21.)

I replaced the second white box, but for the red slide I substituted a plain glass one. A bee found it almost immediately, probably one of the earlier visitors. The slide was now carried to a third position and placed upon an unpainted support fifteen feet from each of the white boxes, the three stations forming the angles of an equilateral triangle. Here it was soon found by two bees. The plain glass slide was then placed on the grass in the center of the triangle, where it was quickly discovered by two bees and a third came a little later. The slide was now placed on the grass fifteen feet outside of the equilateral triangle. It was so inconspicuous that a child, who under my direction approached within a foot of it, failed to see it until a bee alighted in the grass. It required twenty minutes for the bees to find it, and perhaps they would not have done so then had it not been near the route they were pursuing in going back and forth to the hive. It is very evident from this experiment that a force of bees searching for nectar or honey are not easily deceived, but perceive very keenly. The slide was in the sunlight and the attractive influences were the reflected light, the yellow color of the honey (it was goldenrod honey, which is amber-colored), and its odor.

In view of the above observations it can excite no surprise that the bees passed readily under the green leaves which Plateau had pinned on top of the *Dahlia capitula*. The factors by which they were guided were memory and the senses of sight and smell. When the bees returned they found the covered dahlias still in their original position, and though they were not bright colored from above they possessed conspicuousness of size and form; and when the bees in flying about saw the form and color of the rays from beneath and perceived the characteristic odor they recognized promptly the presence of dahlia flowers. Plateau's contention that the form and color of the under side of the capitulum, which was plainly visible, exerted no influence because the insects very rarely approached the head from that side, is without force, for the bees never having found the nectar on the under side, directed their flight toward the aperture or passageway under the leaves, remembering that the nectar was obtained from the disc flowers. It is not justifiable, says Kienitz-Gerloff, to infer that the color of uncovered flowers plays no part in attracting insects, because when they are covered the odor continues attractive.[9]

Plateau repeatedly mentions that the covered dahlia heads were visited by species of Vanessa and Pieris as well as by bees; but while it is admitted that the mental attributes of bees exceed those of lepidoptera, yet the conclusion that the latter were influenced by odor alone is unwarranted. When a butterfly thrust its proboscis beneath the leaves it showed perception of the form of the inflorescence and memory of the location of the nectar. In the following experience the butterflies exhibited keener powers of observation than some of the less specialized hymenoptera. The flowers of *Iris versicolor* are pollinated by bees; and the nectar, which is secreted at the base of the sepals, is protected by the arched petaloid styles, so that it can not be obtained by butterflies in the legitimate way. I have seen *Pamphila mystic* Scudd. standing on the ovary below the perianth and sucking the nectar through the crevice between the sepal and the style; while the larger banded red butterfly, *Limenitis disippus* Godt. obtains the nectar in the same way from above. On the other hand, an hymenopter, which escaped capture, carefully examined the center of two flowers but failed to locate the nectar. There is good reason, then, to infer that the butterflies in Plateau's experiments were influenced by the position and form of the dahlia heads and the color of the rays below as well as by the odor. The criticism of Kienitz-Gerloff is also as applicable here as in the case of bees.

The experiments of Plateau with covered dahlia heads, therefore, were not well adapted for the purpose intended, and afford an insufficient basis for drawing the conclusion that bright coloration is not advantageous to flowers.

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[9] Knuth, P. Handbook of Flower Pollination, 1: 205.